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Victoria M. Donovan

Dirac Twidwell

Daniel R. Uden

Tsegaye Tadesse

Brian D. Wardlow

See next page for additional authors

Authors
Victoria M. Donovan, Dirac Twidwell, Daniel R. Uden, Tsegaye Tadesse, Brian D. Wardlow, Christine H. Bielski, Matthew O. Jones, Brady W. Allred, David E. Naugle, and Craig R. Allen

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RESEARCH ARTICLE
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Special Section:
Fire in the Earth System

Key Points:
- All vegetation functional groups exhibited relatively rapid recovery at the biome level
- At the ecoregion level, vegetation recovered to prewildfire levels with the exception of one ecoregion for a single functional group
- Wildfire-driven vegetation degradation appears localized and represents extreme cases within larger wildfires

Supporting Information:
- Supporting Information S1

Correspondence to:
V. M. Donovan,
vdonovan2@unl.edu

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Resilience to Large, "Catastrophic" Wildfires in North America's Grassland Biome

Victoria M. Donovan[1], Dirac Twidwell[1], Daniel R. Uden[1,2], Tsegaye Tadesse[3], Brian D. Wardlow[3,4], Christine H. Bielski[1], Matthew O. Jones[5,6], Brady W. Allred[5,6], David E. Naugle[5], and Craig R. Allen[2]

[1]Department of Agronomy and Horticulture, University of Nebraska, Lincoln, NE, USA, [2]School of Natural Resources, University of Nebraska–Lincoln, Lincoln, Nebraska, USA, [3]National Drought Mitigation Center, School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE, USA, [4]Center for Advanced Land Management Information Technologies, University of Nebraska–Lincoln, Lincoln, NE, USA, [5]W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA, [6]Numerical Terradynamic Simulation Group, University of Montana, Missoula, MT, USA

Abstract Wildfires are ecosystem-level drivers of structure and function in many vegetated biomes. While numerous studies have emphasized the benefits of fire to ecosystems, large wildfires have also been associated with the loss of ecosystem services and shifts in vegetation abundance. The size and number of wildfires are increasing across a number of regions, and yet the outcomes of large wildfire on vegetation at large-scales are still largely unknown. We introduce an exhaustive analysis of wildfire-scale vegetation response to large wildfires across North America's grassland biome. We use 18 years of a newly released vegetation data set combined with 1,390 geospatial wildfire perimeters and drought data to detect large-scale vegetation response among multiple vegetation functional groups. We found no evidence of persistent declines in vegetation driven by wildfire at the biome level. All vegetation functional groups exhibited relatively rapid recovery to pre wildfire ranges of variation across the Great Plains ecoregions, with the exception being a persistent decrease in the abundance of trees in the Northwestern Great Plains. Drought intensity magnified immediate vegetation response to wildfire. Persistent declines in vegetation cover were observed at the scale of single pixels (30 m), suggesting that these responses were localized and represent extreme cases within larger wildfires. Our findings echo over a century of research demonstrating a biome resilient to wildfire.

1. Introduction

Large wildfires are increasing in a number of biomes across the globe (Donovan et al., 2017; Kasischke & Turetsky, 2006; Schelhaas et al., 2003), driving concerns about the risks that changing wildfire regimes pose to ecosystem services. While numerous studies have emphasized the benefits of fire to ecosystems (e.g., Anderson, 1990; Fuhlendorf et al., 2009; Johnstone et al., 2016; Weaver, 1954), large wildfires have also been associated with the loss of ecosystem services and shifts in vegetation abundance and dominance at local scales across multiple biomes (Adams, 2013). For instance, high severity forest fires in the western mountain forests of the United States can drive a shift to shrub- or grassland-dominance (Odion et al., 2010; Savage & Mast, 2005), while wildfire in northern boreal forests can shift forest cover from conifer to deciduous dominance (Beck et al., 2011). Shrub and woodlands that experience high-intensity fire can transition to annual or perennial grass dominance in grassland and savanna biomes (Ansley & Jacoby, 1998; Twidwell et al., 2016). Increasing wildfires in sagebrush biomes have led to shifts from shrub to the annual grass *Bromus tectorum* (Knapp, 1996; Shinneman & Baker, 2009). Large and high-intensity wildfire has also been suggested to increase the risk of desertification, a transition from a vegetated to bare-ground dominated state, in regions in North America, Australia, and the Mediterranean (United States Department of Agriculture (USDA, 2011; Neary, 2009; Rulli & Rosso, 2007). It is currently unclear how the outcomes of shifting large wildfire patterns will manifest across large scales. While the broader theory in landscape ecology is that large wildfires can increase landscape heterogeneity, concerns around "catastrophic" large-scale vegetation degradation driven by wildfire persist (Turner, 2010). Information and sampling protocols at the

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Investigation: Tsegaye Tadesse, Brian D. Wardlow, Matthew O. Jones, Brady W. Allred, David E. Naugle
Methodology: Victoria M. Donovan, Dirac Twidwell, Daniel R. Uden, Tsegaye Tadesse, Brian D. Wardlow
Supervision: Dirac Twidwell
Validation: Victoria M. Donovan, Daniel R. Uden
Visualization: Victoria M. Donovan
Writing - original draft: Victoria M. Donovan
Writing – review & editing: Victoria M. Donovan, Dirac Twidwell, Daniel R. Uden, Tsegaye Tadesse, Brian D. Wardlow, Christine H. Bielski, Matthew O. Jones, Brady W. Allred, David E. Naugle, Craig R. Allen

spatial and temporal scales necessary to capture the complexity of wildfire-driven vegetation change are needed.

A multiscale perspective is required to understand the outcomes of disturbance on ecosystem structure and function (Allen et al., 2014; Peters et al., 2007; Peterson et al., 1998) because the scale of investigation can have a pronounced effect on the observed pattern (Wiens, 1989). For instance, the effects of fire suppression on stand structure can be observed rapidly at small scales, but can take centuries to emerge on the larger landscape (Baker, 1993). Disturbance processes such as wildfire function at broad scales and are characterized by multiscale heterogeneity that cannot be captured solely through local assessment (Turner, 2010). However, tests of ecological theory from a regional or a continental view lag behind finer scale assessments (Heffernan et al., 2014), largely due to limitations in the availability of spatially and temporally extensive information. While it is clear that wildfire can both promote vegetation persistence and cause persistent shifts in vegetation composition at fine scales (e.g., site, stand, and patch; USDA, 2011), broad scale (e.g., landscape, ecoregion, or biome), scientifically based quantifications of wildfire, and vegetation interactions need to be integrated with our understanding of fine-scale ecological responses in order to understand the impacts of large wildfires across biomes.

The United States has experienced rapid increases in the number of large wildfire in recent decades, from the forested west to the central grasslands of the Great Plains (Dennison et al., 2014; Donovan et al., 2017). While it is well documented that fire plays an important role in both forest (Ahlgren & Ahlgren, 1960; Johnstone et al., 2016; Roberts et al., 2020) and grassland (Anderson & Brown, 1986; Bond & Keeley, 2005; Wells, 1970) systems, fears persist around the negative social and ecological consequences of fire, particularly as wildfires increase to unprecedented numbers relative to what has been seen over the last century. Almost 3 billion dollars were spent on fire suppression costs in the United States in 2017 alone (National Interagency Fire Center, 2018). U.S. Ecological Site Descriptions, a national scale land management framework, list fire as the second most common driver of ecological transitions leading to land degradation in rangelands (Twidwell et al., 2013). With continuing climatic change leading to increasing severity and frequency of drought events along with shifts in seasonal warming trends, large wildfires are likely to continue to increase (Jolly et al., 2015; Liu et al., 2010; Westerling et al., 2006). However, biome scale evaluations of wildfire outcomes on vegetation are limited, even in biomes where surges in wildfire activity have already been recorded.

We conduct an exhaustive assessment of vegetation response following all known large wildfires (>400 ha) that occurred between 2000 and 2012 within the U.S. Great Plains. We use a newly released vegetation data set combined with geospatial wildfire perimeter information and drought data to detect broad-scale shifts in vegetation across rangelands in the U.S. Great Plains over an 18-year period among functional groups and across varying drought conditions. The total hectares burned by large wildfire increased by 400% between the decades 1985–1994 and 2005–2014 (Donovan et al., 2017). We assess the persistence of vegetation change following wildfire across a range of drought conditions to infer potential wildfire intensity patterns tied to scales of vegetation response. We test for three signals of wildfire-induced vegetation change. First, we expect that vegetation functional groups (trees, shrubs, annual forbs and grasses, and perennial forbs and grasses) and bare ground cover will respond differently to wildfire immediately following a wildfire event within the perimeter of each fire (Figure 1a). For instance, we anticipate that bare ground cover will increase following wildfire while perennial forb and grass cover will sharply decrease. Second, because fire intensity is influenced by temperature and precipitation (Pyne et al., 1996; Twidwell et al., 2016), we expect that increasing drought severity will magnify the change in percent cover immediately following wildfire across vegetation functional groups and bare ground (Figure 1b). For instance, we anticipate that we will see a greater decrease in perennial forb and grass cover across a wildfire perimeter when a wildfire occurs under more severe drought conditions. Third, we expect to detect nonlinear, persistent changes in vegetation cover, that is, vegetation cover will persist outside of a prewildfire range of variation (ROV; Figure 1c).

2. Materials and Methods

2.1. Data

Vegetation land cover data was sourced from Jones et al. (2018), which contains yearly, Landsat-derived, 30-m resolution, percent cover estimates for seven land cover classes in western United States rangelands

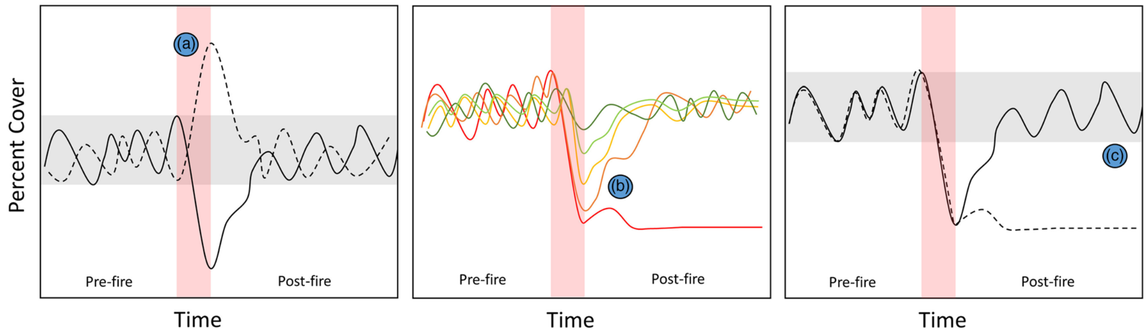

Figure 1. Predicted outcomes of the impacts of large wildfire on vegetation. We expect (a) a functional group-specific response to wildfire immediately following a wildfire event, indicated by the shaded red area, where the solid and dashed lines represent two different functional groups. (b) Because fire intensity is influenced by temperature and precipitation, we monitored the differential response to wildfire within a single functional group based on the severity of drought conditions during the wildfire. Drought conditions are indicated by differing colored lines, where the red line indicates change in functional group cover when wildfire occurred under extreme drought conditions while dark green line represents change in functional group cover when wildfire occurred under moist conditions. (c) We assessed postfire response in relation to the prefire range of variability, indicated by the shaded gray area, to determine if functional group cover returned to the prefire range of variability following wildfire or if vegetation cover persisted outside of the prefire range of variability following wildfire.

from 1984 to 2017: annual forbs and grasses, bare ground, litter, perennial forbs and grasses, rocks, shrubs, and trees, with rangelands delineated according to Reeves and Mitchell (2011). This represents an unprecedented land cover data set for ecological research by providing a long time-series history of high-spatial resolution land cover patterns on an annual time step across a biome. In this study, we excluded litter and rock, which reduced the number of land cover classes analyzed to five.

Remotely sensed, large wildfire perimeter data (delineation of fires >400 ha) from the Monitoring Trends in Burn Severity (MTBS) database were utilized to spatially define individual fires for analysis (MTBS Project, 2019). MTBS is the most comprehensive large wildfire data set in North America, composed of wildfire perimeter data across both public and private lands within the conterminous United States. Wildfire perimeters are mapped in a vector format using differenced Normalized Burn Ratio (dNBR), calculated from prefire and postfire Landsat imagery. Perimeter data were utilized for all large wildfires that occurred from 2000 and 2012 to align with the availability of vegetation and drought data (Figure S1). A total of 1,390 wildfires were included in this analysis.

Monthly Palmer Drought Severity Index (PDSI) data derived from in situ, weather station observations were acquired from the Drought Risk Atlas at the National Drought Mitigation Center between 2000 and 2012 to determine severity. PDSI is calculated using monthly temperature and precipitation data along with information on the water-holding capacity of soils (Palmer, 1965). Though it has known limitations (i.e., the algorithm lacks incorporation of information on important drivers of evapotranspiration; Alley, 1984; Riley et al., 2013; Sheffield et al., 2012), PDSI is one of the most commonly used drought indices in fire literature (e.g., Hessl et al., 2004; Heyerdahl et al., 2008; Riley et al., 2013; Roos et al., 2018; Swetnam & Betancourt, 1998). Thus, it allowed our analysis to be comparable with smaller scale studies across the Great Plains.

Ecoregions from the U.S. Environmental Protection Agency (EPA) were used to designate our study regions. Ecoregions are hierarchical spatial subdivisions that create a stratified landscape based on similarities between ecosystems and environmental response to disturbance (Bryce et al., 1999). The Level I Great Plains ecoregion was used to designate the Great Plains within the conterminous United States. Level III (L3) ecoregions were used to divide the Great Plains into smaller scale subgroups with similar ecosystem properties and vegetation types.

2.2. Analysis

Each wildfire that occurred within the Great Plains L1 ecoregion was classified into its corresponding L3 ecoregion and assigned a PDSI value based on the drought conditions that occurred at the time of the wildfire (Figure S2). To assign a drought condition to each wildfire, we selected the nearest weather station to each wildfire perimeter that reported PDSI values for that wildfire's estimated start date. We used National Oceanic and Atmospheric Administration (NOAA) PDSI categories to create moisture classes across PDSI values. PDSI values ranging from: −4 or less were categorized as extreme drought, 3 to −3.9 were categorized as severe drought, −2 to 2.9 were categorized as moderate drought, −1.9 to 1.9 were categorized as near normal, and 2 or more were categorized as moist conditions.

For each year from 2000 to 2017, we used Google Earth Engine (Gorelick et al., 2017) to calculate mean percent cover among all 30-m rangeland pixels within each wildfire perimeter for each of the following functional groups: perennial forbs and grasses, annual forbs and grasses, trees, shrubs, and bare ground. For the same set of years and plant functional groups, we then calculated the mean percent cover across wildfire perimeters for the L1 Great Plains and L3 ecoregions. Only L3 ecoregions that had 10 or more large wildfires were included in our L3 ecoregion assessment. On average, perennial forb and grass cover dominated wildfires across the Great Plains over our study period (Table S1). Bare ground and annual cover were the next most prevalent cover types on average within wildfire perimeters, while shrub and tree cover had the lowest mean cover during our study period (Table S1).

We assessed post wildfire vegetation recovery within each functional group at the Great Plains (L1) and ecoregion (L3) level. Historical ROV has been used in previous research to identify persistent shifts in ecosystem configurations (Keane et al., 2018; Scheffer & Carpenter, 2003; Seidl et al., 2016). To calculate prefire ROV, we used average annual vegetation cover from 10 years prefire. We calculated the average percent cover across wildfires for each year that data were available along with estimates of standard error. The minimum and maximum percent cover values calculated from prefire annual standard error estimates were used to designate the upper and lower bounds of the prefire ROV. Following wildfire, functional group cover that persists outside of the prefire ROV are indicative of a persistent wildfire driven shifts in vegetation, while a return of functional group cover to the prefire ROV are indicative of vegetation recovery (Figure 1; Scheffer & Carpenter, 2003). Changes that occurred following wildfire (for instance, a persistent decline in vegetation cover outside the prefire ROV that occurred 5 years after fire) were predicted to be driven by an alternative event (e.g., agricultural conversion or woody encroachment management) and were not considered to be wildfire driven.

Data were further subdivided at both the Great Plains (L1) and individual ecoregion spatial extents (L3) into the five PDSI categories based on PDSI conditions that occurred at the time of the wildfire. Fire intensity can be strongly influenced by temperature and precipitation, with drought increasing fire intensity, leading to more extreme fire conditions and greater fire severity (Pyne et al., 1996; Twidwell et al., 2016). Thus, vegetation response immediately following wildfire, along with post wildfire recovery patterns, were investigated for each drought category to determine if there was a different within-functional group response to wildfire based on drought conditions during wildfire.

To evaluate our approach, we isolated four large wildfires where we expected to see persistent declines in vegetation cover based on their ecosystems, previous studies, wildfire policies, and patterns observed in our data set. These included the 2012 Ash Creek wildfire that burned through the Northern Cheyenne Reservation in Montana, the 2012 Region 24 Complex fire that burned though the Niobrara River valley in Nebraska, the 2006 East Amarillo Complex fire in the Panhandle of Texas, and the 2011 Ferguson Fire in that burned the Wichita Mountain Wildlife Refuge in Oklahoma. We calculated annual mean percent cover across each wildfire perimeter for perennial forbs and grasses, annual forbs and grasses, trees, shrubs, and bare ground. Google Earth Engine was then used to calculate the percent change between the percent cover of each functional group in 2017 and at time since fire (TSF) of −1 (i.e., the year preceding the fire) for each pixel within each wildfire. We then examined percent cover values over time in pixels that exhibited the greatest percent change between the year preceding wildfire and 2017 to assess vegetation recovery. We assessed changes in tree cover in the Ash Creek wildfire, where ponderosa pine (*Pinus ponderosa*) was prevalent. Ponderosa pine ecosystems have been shown to be susceptible to ecological transitions (a shift in ecosystem structure, function, and feedbacks) following severe wildfire (Odion et al., 2010; Roberts et al., 2019). In the Region 24 Complex fire, we assessed perennial forb and grass cover, due to the perceived fragility of the Nebraska Sandhills grasslands to erosion following wildfire (USDA, 2011). Shrub cover was assessed in the East Amarillo Complex fire because of the extreme drought conditions under which it occurred (PDSI = −5.01 at nearest weather station). Fire in extreme drought can decrease shrub cover (Twidwell et al., 2016). Annual forb and grass cover was assessed in the Ferguson fire, as it fell within an ecoregion where there was strong change in annual cover immediately following wildfire in wildfire-scale ecoregion assessments.

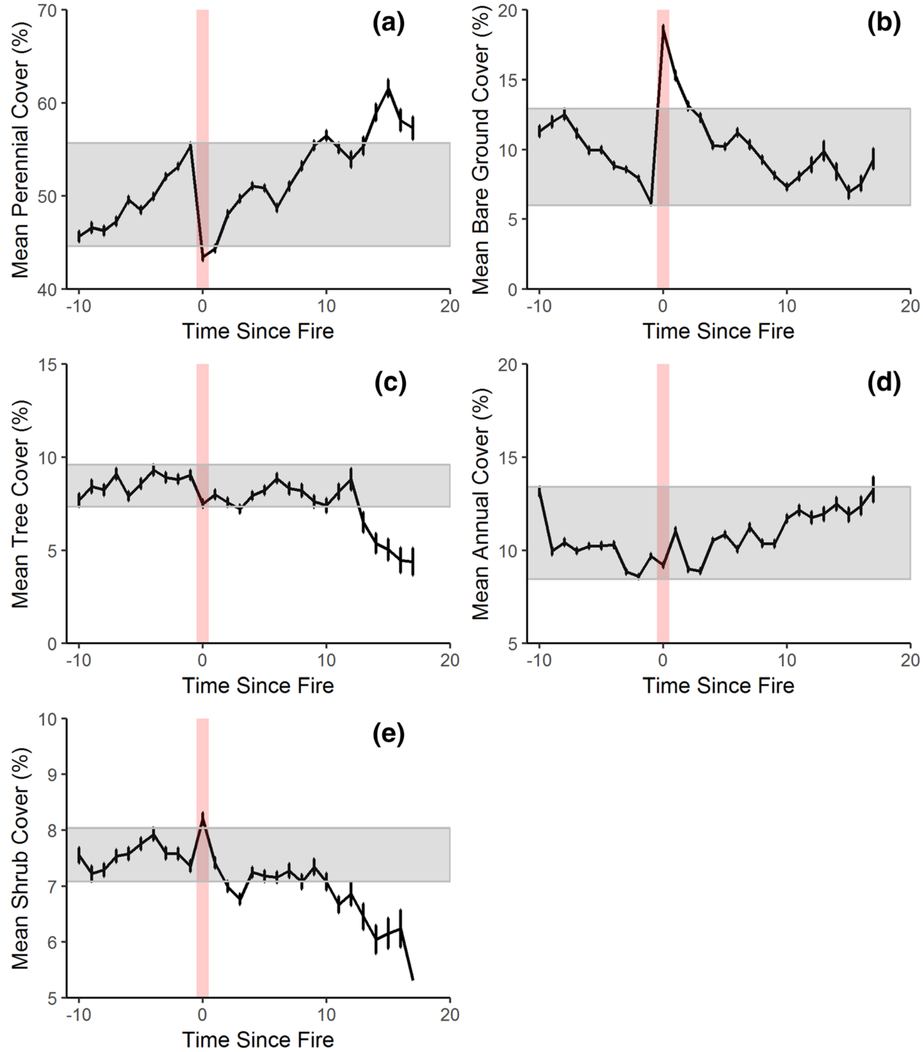

Figure 2. The change in mean cover relative to time since fire for (a) perennial forbs and grasses, (b) bare ground, (c) trees, (d) annual forbs and grasses, and (e) shrubs in the Great Plains. The red shaded bar indicates the year the wildfire occurred. The gray shaded bar indicates the range of variation in cover that occurred 10 years before the wildfire. Error bars represent standard error. The scale of the *y*-axis varies by functional group.

3. Results

3.1. Vegetation Responses Following All Wildfires

Localized, immediate response of vegetation functional groups and bare ground cover to wildfire were so recurrent within wildfire perimeters that we were able to detect them across the Great Plains. Among all functional groups, perennial forbs and grasses experienced the most drastic declines in cover immediately following wildfire, falling outside of the prefire ROV (Figure 2a). Correspondingly, bare ground saw the greatest spike in cover immediately following wildfire (Figure 2b). Mean tree cover also declined immediately following wildfire in the Great Plains (Figure 2c). In contrast, mean annual cover responded minimally to wildfire, with a slight decline immediately following wildfire in the Great Plains (Figure 2d). Shrub cover increased immediately following wildfire (Figure 2e).

Drought similarly had a recurrent localized impact on vegetation response to wildfire in functional groups by influencing the magnitude of change in cover. The decline in perennial forb and grass cover immediately following wildfire varied greatly between moist, near normal, and drought conditions, where declines in perennial forb and grass cover were greater as PDSI decreased during wildfire (Figure 3a). Bare ground cover

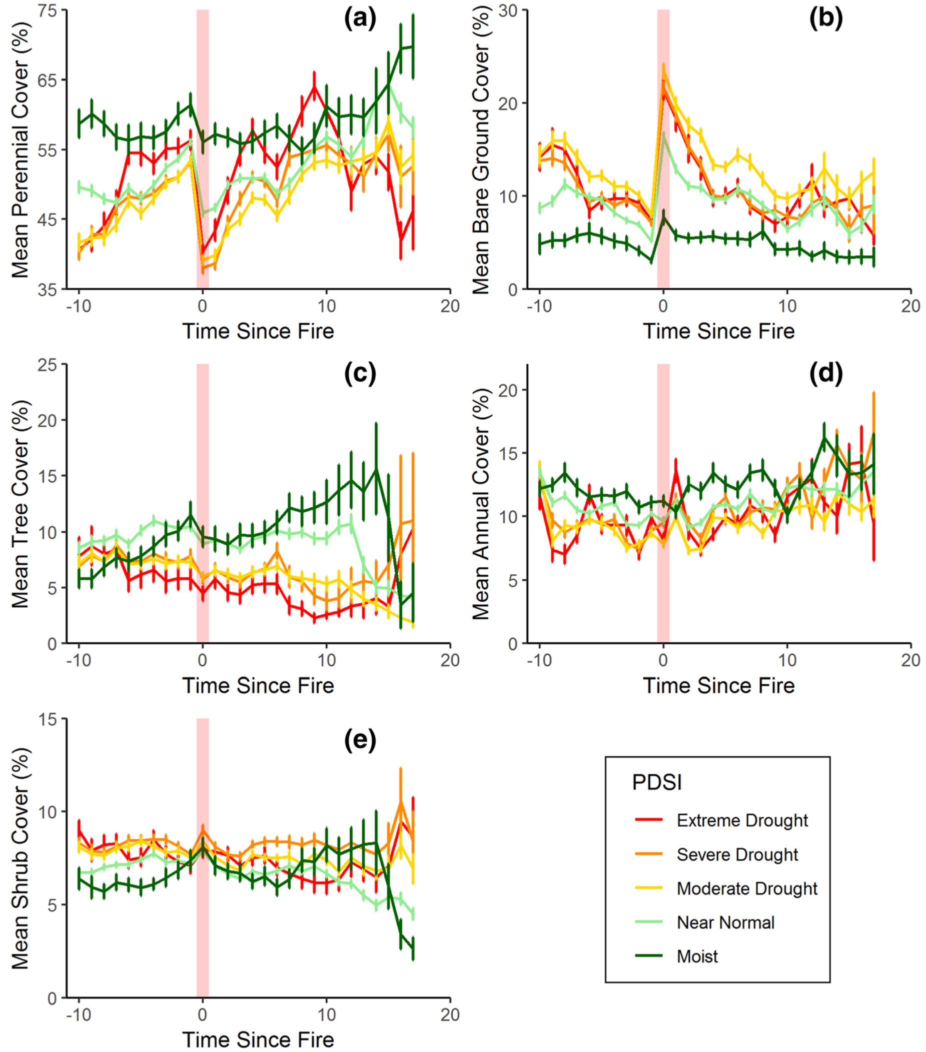

Figure 3. The change in mean cover relative to time since fire for (a) perennial forbs and grasses, (b) bare ground, (c) trees, (d) annual forbs and grasses, and (e) shrubs in the Great Plains relative to drought condition. The red shaded bar indicates the year the wildfire occurred. Error bars represent standard error. The scale of the *y*-axis varies by functional group.

mirrored patterns seen in perennial forb and grass cover (Figure 3b). Mean percent tree cover was differentiated by PDSI category prior to the wildfire and did not respond strongly to differences in PDSI in relation to wildfire, suggesting that it responded independently of fire to drought condition (Figure 3c). Annual forb and grass cover showed no response to wildfire during moist conditions, while slight declines were seen at near normal, moderate, and extreme drought conditions (Figure 3d). There was no strong relationship between the magnitude of change in shrub cover in relation to PDSI in the Great Plains (Figure 3e).

No persistent changes in vegetation cover occurred following wildfire in any functional group in the Great Plains. In each functional group, vegetation cover remained within or returned to prefire ROV over a short time following wildfire (Figure 2). This did not change with respect to drought condition (Figure 3).

3.2. Ecoregion Differences in Vegetation Response

Regardless of ecoregion, perennial forb and grass cover had the greatest declines in percent cover immediately following wildfire of all functional groups (Figure 4). However, certain ecoregions had more

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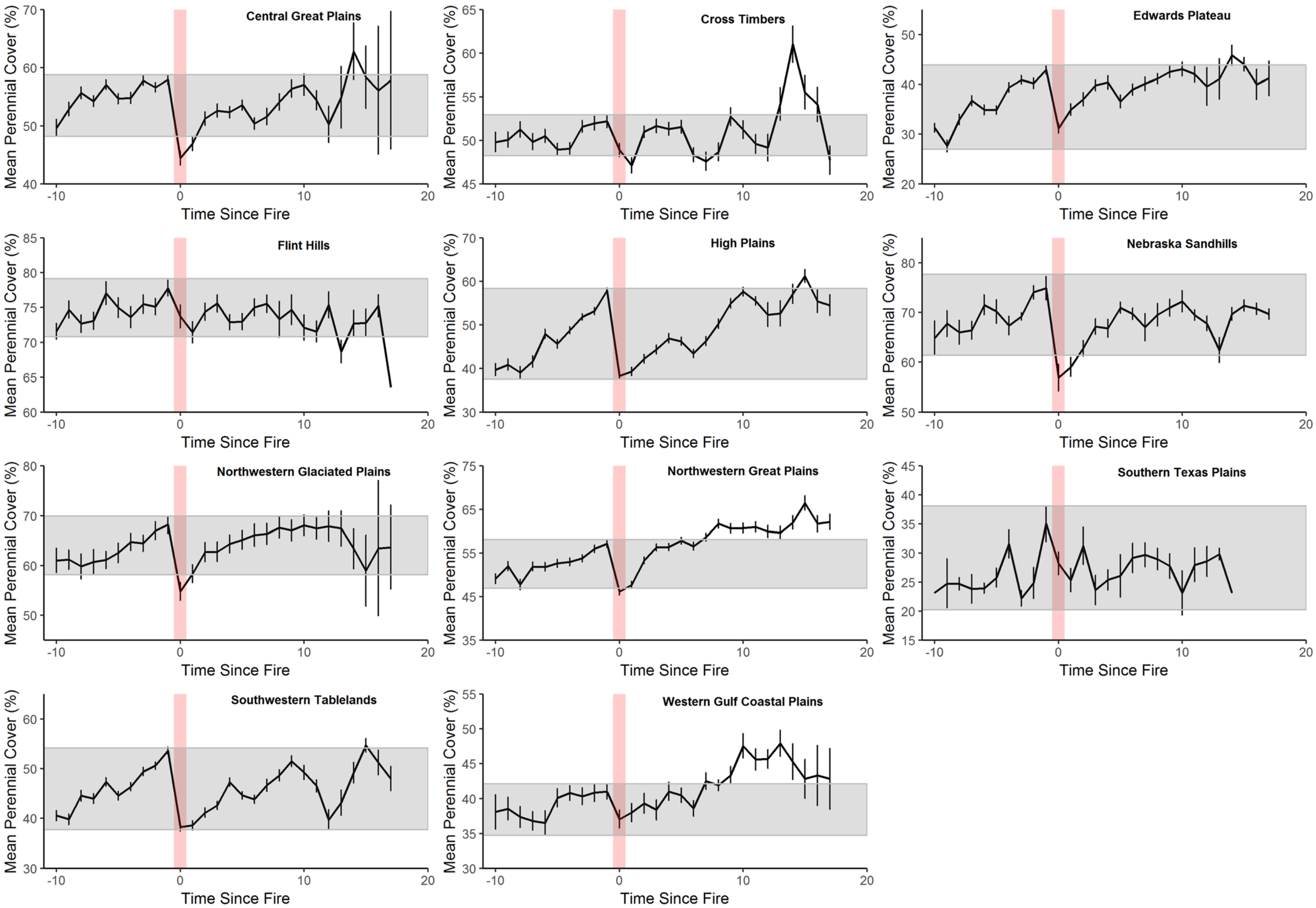

Figure 4. The change in mean perennial forb and grass cover relative to time since fire across level 3 ecoregions. The red shaded bar indicates the year the wildfire occurred. The gray shaded bar indicates the range of variation in cover that occurred 10 years before the wildfire. Error bars represent standard error. The scale of the *y*-axis varies by ecoregion.

substantial declines in perennial forb and grass cover than others (Figure 4). For instance, the Nebraska Sandhills, Northwestern Glaciated Plains, Northwestern Great Plains, Cross Timbers, and Central Great Plains all had perennial forb and grass cover that declined outside the prefire ROV. Declines in perennial forb and grass cover corresponded with large increases in bare ground cover across these ecoregions (Figure 5). Change in tree cover following wildfire was more variable at the ecoregion scale (Figure 6). The Flint Hills and Northwestern Glaciated Plains showed slight increases in tree cover immediately following wildfire, while the High Plains and Nebraska Sandhills demonstrated no notable change. Ecoregions that had higher amounts of mean tree cover generally experienced declines in tree cover immediately following wildfire. This became more evident when we limited our assessment to wildfire perimeters that contained 10% or more tree cover the year before wildfire, where all ecoregions demonstrated an average decrease in tree cover immediately following wildfire (Figure S3). Like tree cover, mean annual forb and grass and mean shrub response varied by ecoregion (Figure S4; Figure S5). Regions like the High Plains and Cross Timbers had slight declines in mean annual forb and grass cover immediately following wildfire, while the Nebraska Sandhills had an increase in annual forb and grass cover immediately following wildfire (Figure S4). In all ecoregions however, changes fell within the prefire ROV of yearly annual forb and grass cover. Ecoregions like the Central Great Plains, Flint Hills, and Northwestern Great Plains had a strong spike in shrub cover immediately following wildfire, while regions like the High Plains showed minimal response in shrub cover to wildfire (Figure S5).

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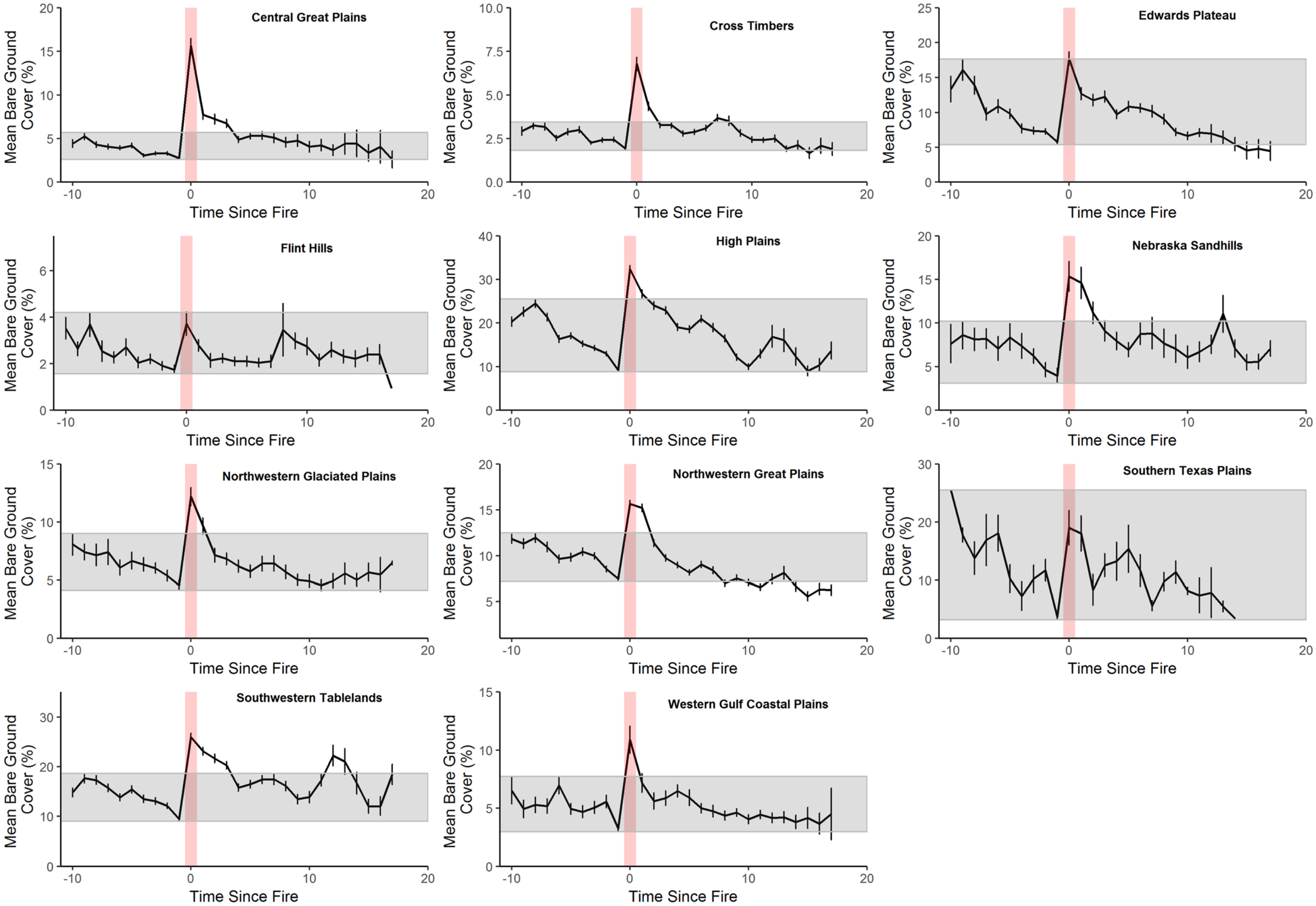

Figure 5. The change in mean bare ground cover relative to time since fire across level 3 ecoregions. The red shaded bar indicates the year the wildfire occurred. The gray shaded bar indicates the range of variation in cover that occurred 10 years before the wildfire. Error bars represent standard error. The scale of the *y*-axis varies by ecoregion.

Perennial forb and grass cover response to wildfire in relation to drought condition was fairly consistent across ecoregions, where decreases in perennial forb and grass cover immediately following wildfire were greater as PDSI decreased (Figure S6). Bare ground cover correspondingly increased as PDSI decreased, regardless of ecoregion (Figure S7). There were no strong patterns between declines in percent tree cover in relation to PDSI in any ecoregion (Figure S8). This did not change when we limited our assessment to wildfire perimeters that contained 10% or more tree cover the year before wildfire (Figure S9). The response of annual forb and grass percent cover to wildfire was tied to drought conditions in some ecoregions, like the Western Gulf Coastal Plain and the Southwestern Tablelands, while patterns related to PDSI were indistinguishable in other regions (Figure S10). Like in the Great Plains as a whole, there was no strong relationship between the magnitude of change in shrub cover in relation to PDSI across ecoregions (Figure S11).

Persistent changes in vegetation cover were not evident in most functional groups when assessed at the ecoregion scale (Figures 4–5 and S3–S5) regardless of drought condition (Figures S6–S11). Tree cover in the Northwestern Great Plains was an exception to this, where declines in mean tree cover persisted, irrespective of the amount of tree cover that was present before fire (Figures 6 and S3), and of drought condition during fire (Figures S8 and S9).

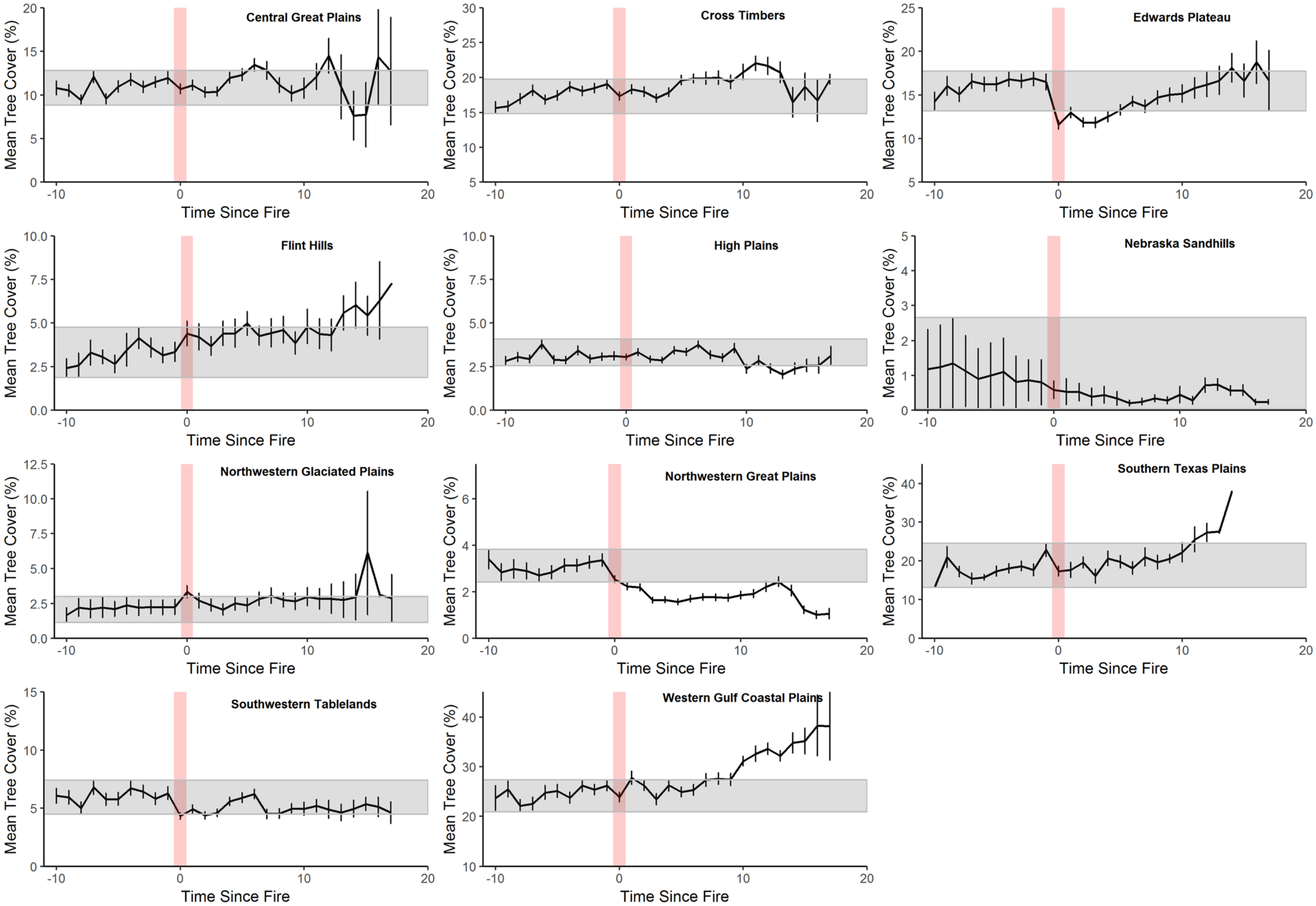

Figure 6. The change in mean tree cover relative to time since fire across level 3 ecoregions. The red shaded bar indicates the year the wildfire occurred. The gray shaded bar indicates the range of variation in cover that occurred 10 years before the wildfire. Error bars represent standard error. The scale of the *y*-axis varies by ecoregion.

3.3. Pixel-by-Pixel Vegetation Response to Selected Iconic Wildfires

Perennial forb and grass response within our selected wildfires was similar to that seen when wildfire trends were summarized at the ecoregion and biome level, with a sharp decline in perennial forb and grass cover immediately following wildfire and then a rapid increase in subsequent years (Figure 7). This decline similarly corresponded with a sharp spike in bare ground across all but the Ferguson wildfire (Figure 7). In the Ferguson wildfire, the decline in perennial forb and grass cover corresponded with a sharp increase in annual forb and grass cover. These patterns aligned with TSF = 1 rather than TSF = 0 (like in other assessments), likely due to the late timing of input imagery for the land cover data set. Annual forb and grass cover declined immediately following wildfire in both the Region 24 Complex wildfire and the East Amarillo Complex wildfire, while it increased in the Ash Creek wildfire (Figure 7). Tree cover declined immediately following wildfire in all wildfires except for East Amarillo Complex, which showed a slight increase in tree cover following wildfire (Figure 7). Shrub cover similarly showed a variable response, with an increase in shrub cover immediately following wildfire in the Ferguson, Region 24 Complex, and Ash Creek wildfires, and a decrease in the East Amarillo Complex wildfire (Figure 7).

No persistent changes occurred in perennial forbs and grasses, annual forbs and grasses, or shrubs in any of the four wildfire perimeters assessed. However, tree cover appeared to show a persistent decline in both the Ash Creek and Region 24 Complex wildfires. Within these wildfires, there was a high level of variability in

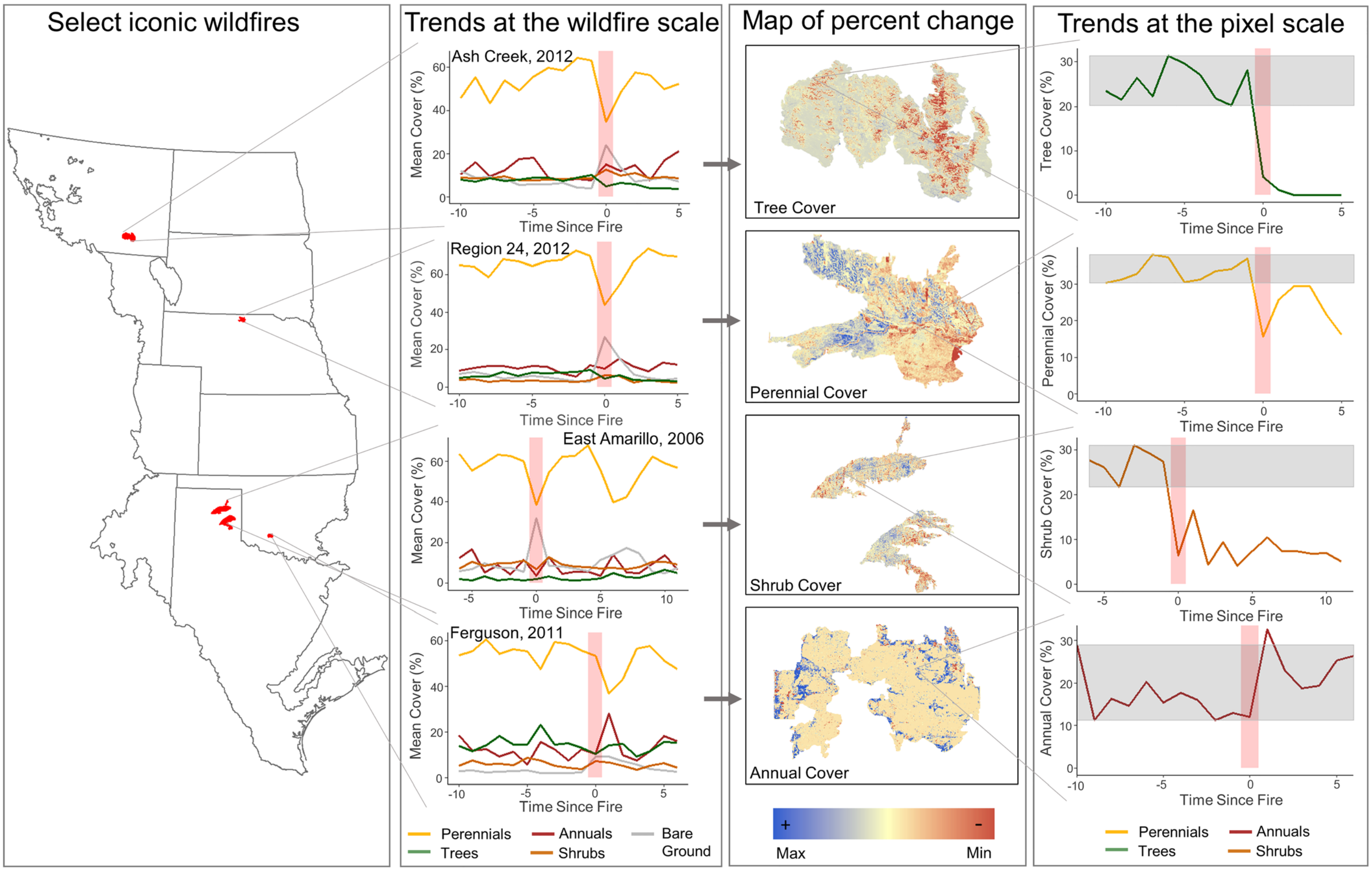

Figure 7. Assessment of the change in percent cover within the Ash Creek, Region 24 Complex, East Amarillo Complex, and Ferguson wildfire perimeters. The first column displays the locations of the wildfires (red) within our Great Plains study area. The second column displays yearly mean annual forbs and grasses, bare ground, perennial forbs and grasses, shrub, and tree percent cover relative to time since fire (TSF) within each wildfire perimeter. The third column displays maps of the yearly percent cover of trees (Ash Creek fire), perennial forbs and grasses (Region 24 Complex fire), shrubs (East Amarillo Complex fire), and annual forbs and grasses (Ferguson fire) calculated by subtracting the percent cover at TSF = −1 and the percent cover of the last year of analysis (2017). The fourth column shows the change in percent cover for a single pixel within the wildfire perimeter that has a high percent change based on subtracting the percent cover at TSF = −1 and the percent cover of the last year of analysis (2017).

pattern across pixels among all functional groups and wildfires. Although persistent changes were not observed across individual wildfires, they were identifiable at the local pixel scale. Searching among pixels that had the highest levels of percent change following wildfire, we identified a pixel with a persistent decline in tree cover from an average of 25% ± 1.21 standard error (SE) to 0% following the Ash Creek wildfire (Figure 7). Similarly, we found a persistent decline in shrub cover in the East Amarillo Complex wildfire, with an average of 27% $\pm$ 1.31 SE before wildfire to an average of 8% ± 1.04 SE (Figure 7). Although we were able to identify pixels with perennial forb and grass cover that remained below the prefire ROV in cover observed before TSF = 0 following the Region 24 Complex fire, perennial forb and grass cover appears to rebound to near prefire levels before declining again (Figure 7). This suggests that perennial forbs and grasses in these pixels were likely responding to an additional disturbance event rather than showing a persistent change driven by wildfire occurrence. In the Ferguson wildfire, we noted an increase in annual forb and grass cover following wildfire (Figure 7). However, this was not outside of the prefire ROV.

4. Discussion

We found no evidence of persistent shifts in vegetation cover driven by wildfire in the Great Plains. All vegetation functional groups exhibited relatively rapid recovery to prewildfire ROV, with the single exception being a persistent decrease in the relative abundance of trees in the Northwestern Great Plains ecoregion. Persistent shifts in vegetation cover were observed primarily at the scale of single pixels (30-m level of analysis), suggesting that persistent wildfire driven shifts in vegetation composition are localized and represent extreme cases within larger wildfires. This contrasts with the perception that vast areas are being homogenized or destroyed by large "catastrophic" wildfire disturbances. Fire has had an enduring presence in the Great Plains and has long been recognized for playing an important stabilizing role in grasslands (Anderson & Brown, 1986; Weaver, 1954; Wells, 1970). Over a century of field studies support the rapid regeneration of grasses following fire (e.g., Briggs & Knapp, 1995; Vermeire et al., 2011; Weaver, 1935). Our findings build off field-based analyses to help further confirm the Great Plains as a biome largely resilient to wildfire.

Grasses and forbs recovered rapidly following wildfire in the Great Plains. Perennial forb and grass cover decreased the most drastically of all functional groups assessed immediately following wildfire; however, it consistently recovered to the prefire ROV. The Nebraska Sandhills ecoregion is suggested to be particularly sensitive to wildfire, with state and transition models predicting that a loss of grassland vegetation from fire will lead to an active blow out (also known as a bare ground state experiencing active wind erosion; USDA, 2011). However, we found that, like other ecoregions, perennial forb and grass vegetation regenerated rapidly in the Nebraska Sandhills. These findings match with a number of local field-based studies demonstrating perennial forb and grass recovery following wildfire (e.g., Arterburn et al., 2017; Rideout-Hanzak et al., 2011) and increased vigor of grasses following fire and drought (Knapp, 1985). Mean annual forb and grass cover did not respond strongly to wildfire relative to yearly variation in mean cover through time, suggesting that variation in annual forb and grass cover was likely influenced by other environmental factors. In addition to fire, annual forb and grass cover has been shown to be influenced by factors like grazing (e.g., Hayes & Holl, 2003) and climate (e.g., Mack & Pyke, 1984), which may have played a more predominant role in shaping annual forb and grass cover patterns observed at large scales. It is important to note that currently available data do not allow us to track the potential for within functional group transitions, such as shifts from a native to invasive annual grass. In a local field-based study, Ratajczak et al. (2019) noted a shift in the dominance of grasses versus forbs following wildfire during drought, which we could not assess. Continued advancements in data products will allow us to better unravel these complexities.

Woody species showed mixed responses to wildfire. Trees were the only functional group to show a persistent change in cover within an ecoregion (though not across the entire biome). This pattern was confirmed with our pixel-by-pixel analysis. Forested areas in the Northwestern Great Plains, where a persistent decrease was observed, are largely composed of nonresprouting ponderosa pine in contrast with ecoregions like Cross Timbers and the Southern Texas plains, which are dominated by resprouting tree species like oak (*Quercus* sp.). Ponderosa pine has been shown to be susceptible to state changes in smaller scale, field-based studies (e.g., Odion et al., 2010; Roberts et al., 2019; Savage & Mast, 2005). That said, ponderosa pine regeneration occurs over decadal time scales rather than the annual patterns captured here, so longer term assessments may be needed to assess recovery relative to the life history of this species. Interactions with additional factors such as postfire management treatments (Lindenmayer & Noss, 2006), insect outbreaks (Davis et al., 2012), and drought-induced dieback (Hember et al., 2017) may also alter long-term patterns in woody recovery and persistence, though these factors were not assessed here. In contrast, we did not identify any persistent changes in shrub cover at the Great Plains or ecoregion level. Persistent shifts in shrub cover were only found in our pixel-by-pixel analysis. Resprouting shrub species are generally unresponsive to low-intensity fires that occur in the absence of browsers in local field-based studies (O'Connor et al., 2020; Ratajczak et al., 2014), while high-intensity fire can drive a decrease in shrub cover (Ansley & Jacoby, 1998; Twidwell et al., 2016). Our results likely reflect some of this heterogeneity in fire intensity created by wildfire. Typical characterizations of wildfire are implemented at scales similar to the pixel level of our assessment (e.g., 30- to 100-m sampling transects; Roberts et al., 2019; Wester et al., 2014). Scaling these findings up to a wildfire, region, or biome does not always accurately depict the outcomes of wildfire on vegetation outcomes. Our findings emphasize the need to consider sampling bias in relation to small-scale or plot based assessments of wildfire outcomes when generalized to the larger landscape. Characterizing variation in vegetation response across a wildfire perimeter and across a range of scales will be important for understanding the impacts of changing large wildfire occurrence on Great Plains ecosystems in the future.

A more nuanced assessment of the relationships between variability in drought, vegetation, and wildfire is needed in the Great Plains to fully gauge the outcomes of large wildfires. Numerous small-scale studies have documented the complex interactions between drought, fire, and vegetation composition (e.g., Fuhlendorf & Smeins, 1997; Ratajczak et al., 2019; Taylor et al., 2012; Twidwell et al., 2016). Wildfire characteristics like intensity and size are strongly influenced by drought (Krueger et al., 2015; Twidwell et al., 2016); however, the impacts of drought on fire are spatially and temporally heterogeneous. Factors like topography and vegetation structure alter fire behavior, preventing homogenous responses of wildfire to drought (Finney, 2005; Twidwell et al., 2009; Viedma et al., 2015). For instance, variation in fuel distribution and type play a large role in determining spatial heterogeneity in fire intensity (Hobbs & Atkins, 1988; Turner, 2010). Higher fuel loads near trees or shrubs are more likely to create the fire intensity necessary to consume woody vegetation (Thompson & Spies, 2009; Twidwell et al., 2009, 2016), and greater tree densities are more likely to promote crown fire spread (Wagner, 1977), which can drive transitions in woody systems (e.g., Odion et al., 2010). This aligns with the weaker relationships we observed between wildfire and changes in tree cover when tree cover was low, regardless of drought condition. Variation in fuels at a scale as small as 1 m^2 can produce substantial differences in local fire intensity (Thaxton & Platt, 2006). Even though the fire intensity necessary to consume grasses is much lower than trees and shrubs (Twidwell et al., 2013), we found relatively high levels of mean perennial forb and grass cover following wildfire. This suggests heterogeneity within the fire perimeter resulted in a large proportion of perennial forb and grass cover remaining unburned (>40% on average) or that grass cover recovered quite rapidly, regardless of drought condition. Numerous studies have documented shifts in perennial species abundance following fire (e.g., Abrams & Hulbert, 1987; Silletti & Knapp, 2002) and rapid recovery could be attributed to shifts in perennial grass species dominance, for instance from a mesic to more xeric grass species.

The inability to monitor fire intensity across expansive areas limits our ability to discern patterns in spatial and temporal heterogeneity; however, continued advancements in remote sensing technology will allow us to more thoroughly capture such complexity. Currently, fire intensity is not measured directly and is instead usually inferred from remotely sensed proxy measurements. Most surrogate measures for fire intensity, such as fire severity and drought measures, are sensitive to changes in vegetation functional groups and lack the proper accuracy to delineate spatial–temporal patterns. Fire severity classifications are easily confounded across vegetation types (Hammill & Bradstock, 2006; Kolden et al., 2015). MTBS fire severity classifications lack ecological associations (i.e., a dNBR value of 500 is associated with a specific conifer group that experienced 80% tree mortality), making them difficult to compare across wildfires (Kolden et al., 2015). Similarly, high-resolution, remotely sensed climate data available to ecologists tend to be associated with vegetation condition (e.g., enhanced vegetation index, normalized difference vegetation index, Vegetation Condition Index , and Vegetation Drought Response), making them difficult to use to unbiasedly assess wildfire–vegetation interactions across large areas that host different vegetation communities. Other indicators of drought that have been linked to wildfire trends, such as soil moisture (Krueger et al., 2015), tend to be too limited by low-spatial resolution that is not well suited for fine-scale assessment of vegetation response to wildfire (Peng et al., 2017). For instance, the NASA Soil Moisture Active Passive and European Space Agency Soil Moisture Ocean Salinity instrument provides soil moisture estimates but with relatively low-spatial resolution (~25 km). That said, new remotely sensed observations, ecological transition identification methods (Uden et al., 2019), and increasingly fine-scale, large-extent remotely sensed information (Jones et al., 2018) continue to advance our ability to study large-scale ecosystem complexity and can build upon the initial exploration of the 1,390 wildfires analyzed in this study.

Vegetation loss and erosion following fire remains a concern among rangeland stakeholders (e.g., Shore, 2019). However, relatively rapid vegetation recovery across broad scales brings to question postfire management tactics that assume high plant mortality and persistent bare ground caused by wildfire. For instance, erosion mitigation tactics like reseeding and grazing deferment are sometimes used following wildfire to assist with rehabilitating burned sites (Gates et al., 2017; Hardegree et al., 2011; Tanaka et al., 2011). Following the 2012 and 2017 wildfire years in Texas, millions of dollars in disaster assistance were offered to assist with vegetation recovery and erosion mitigation like reseeding, cross fencing, and grazing deferment (Natural Resources Conservation Service [NRCS] Texas, 2012, 2017). Reseeding programs made up an average of 7% of USDA NRCS expenditures from 2005 to 2009 (Twidwell, Allred, & Fuhlendorf, 2013), and continue to be promoted in Great Plains rangelands to help stabilize regions perceived as vulnerable following wildfire (e.g., Fick, 2017; Fick et al., 2017). Our results support local, field-based studies that question the necessity of such programs in the Great Plains (e.g., Arterburn et al., 2017; Gates et al., 2017). Great Plains grasslands have evolved with fire (Anderson, 1990, 2006; Wells, 1970), and grasses have substantial ability to survive and resprout through bud bank following fire (Dalgleish & Hartnett, 2009; Pausas & Paula, 2020). We similarly found no large increase in annuals following wildfires, demonstrating that although more arid rangelands may benefit from tactics like reseeding treatments to mitigate for invasion by nonnative annual grasses (e.g., Knutson et al., 2014; Kulpa et al., 2012), alternative uses of funds, such as woody fuels management, may be more beneficial to inhabitants of the Great Plains.

Social-ecological systems are nonstationary (Craig, 2010; Preiser et al., 2018), and under the changing global environment, the trajectory of global change drivers like wildfire and their impacts on social-ecological systems is uncertain. Projected changes in drought patterns (Dai, 2013; Wehner et al., 2011) along with associated increases in wildfire (Abatzoglou & Williams, 2016) suggest that future wildfire and drought will likely function outside the historical range of variability that we assessed in this study. Continued assessments of vegetation response to wildfire across a range of scales, from local, field-based studies, to biome wide approaches, will be needed to understand the outcomes of shifting wildfire patterns.

Data Availability Statement

Wildfire data were generated by the Monitoring Trends in Burn Severity (MTBS) project (www.mtbs.gov), supported by the USDA Forest Service Remote Sensing Applications Center (RSAC) and the USGS Earth Resource Observation Systems (EROS) Data Center, and can be accessed at www.mtbs.gov. Ecoregion divisions were generated by the Environmental Protection Agency (EPA) and can be accessed at www.epa.gov. PDSI drought data were generated by and can be accessed from the Drought Risk Atlas at the National Drought Mitigation Center (https://droughtatlas.unl.edu/). Vegetation data can be accessed from the Rangeland Analysis Platform (https://rangelands.app/).

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